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GYNANDROMORPHISM IN SALTATORIAL ORTHOPTERA, WITH THE DESCRIPTION OF AN ADDITIONAL FIELD-COLLECTED SPECIMEN

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Abstract.—A thorough review of gynandromorphism in the saltatorial Orthoptera indicates that of a total of 522 records, 47 specimens are clearly bilateral gynandromorphs. Gynandromorphism has been reported for one species in the Tetrigidae, 24 species in the Acrididae, one species in the Gryllacrididae, six species in the Gryllidae, and 21 species in the Tettigoniidae (including a new case in *Microcentrum retinerve* (Burmeister) described herein). Although it is doubtful that gynandromorphism has adaptive significance, the phenomenon appears in unusually high frequencies for at least two species.

Bilateral gynandromorphism is infrequently reported in the literature and no doubt is uncommon. Most cases involve species that exhibit pronounced sexual dimorphism as in butterflies (Blanchard, 1969; Hessel, 1964; Schmid, 1973; Tweedie, 1965) in which wing color patterns differ between the sexes, and with beetles (Balazuc, 1948, 1952; Balazuc and Donnot, 1953) in which secondary sexual characters such as mandible morphology, head ornamentation, and length of elytra differ between the sexes. Reviews of this morphological anomaly that mention Orthoptera include Hagen (1861), Bertkau (1889), Uvarov (1966) and Chopard (1938).

Among the Orthoptera (*sensu stricto* the saltatorial Orthoptera: grasshoppers, crickets, and katydids) sexual dimorphism is usually much less pronounced. Besides the obvious differences in external genitalia, the only noticeable difference between males and females involves size, females being larger than males in most species. In addition, among the ensiferan Orthoptera, sex differences in the morphology of the tegmina are common for those species that employ tegminal stridulation in pair formation. It is probable that many cases of bilateral gynandromorphism in the Orthoptera have been overlooked by all but the most discriminating specialist. The first case in the Orthoptera was reported by Brisout de Barneville (1847, 1848a, b). Since then, 66 reports have accumulated describing some level of gynandromorphism in Orthoptera.

In this paper, gynandromorphism in the Orthoptera is reviewed: the species are listed; the degree of gynandromorphism is evaluated; the origin of the specimen, i.e., whether field-collected or derived from a laboratory stock or from interspecific genetic crosses, is indicated; and hypotheses for this phenomenon are reviewed. In addition, a field-collected bilateral gynandromorph of the lesser angle-winged bush katydid, *Microcentrum retinerve* (Burmeister), is described and figured for the first time.

Review of Gynandromorphism

In general the reports of gynandromorphism in Orthoptera describe three degrees of this phenomenon. The first level involves cases in which the specimen is predominantly one sex but with an accessory structure or structures characteristic of the opposite sex (Ramme, 1926; Pearson, 1929; Paul, 1941; Friauf, 1947). The second level involves specimens having several male and female features arranged either randomly or in a non-symmetrical pattern; for example, a grasshopper with ovo-testes (an ovary with spermatocytic tissue) and external features that reflect both male and female characteristics. Such specimens have been called sexual mosaics or intersexes (Ohmachi, 1932; Suzuki, 1933). The third level involves cases in which sexual differentiation is distinct on either side of the plane separating the left and right sides of the body; this is bilateral gynandromorphism.

To date, gynandromorphism has been reported for 24 species of grasshoppers (Acrididae), one species of grouse locusts (Tetrigidae), one species of camel crickets (Gryllacrididae), six species of crickets (Gryllidae), and 21 species of katydids (Tettigoniidae) (Table 1). Of a total of 522 records, 47 specimens were clearly bilateral gynandromorphs. Nearly all of the other records were intersexes derived from laboratory stocks involved in radiation experiments (Suzuki, 1933, 1934) or from hybrid crosses involving either intersexes and normal individuals of the same species (Ohmachi, 1929, 1932) or two different species (Cousin, 1935). Among the bilateral gynandromorphs 13/21 of the Tetrigidae and Acrididae, 10/14 of the Tettigoniidae, and 2/6 of the Gryllidae were male on the left side, female on the right. Although this suggests that the left side is expressed as male in the majority of individuals, it is not possible to say if this is significant, considering the small numbers involved. A *chi*-square analysis, however, suggests there is nearly a 90% probability that this reflects a trend toward maleness on the left ($\chi^2 = 4.78$, df = 3).

The majority of the reported cases of gynandromorphs are descriptions of the external morphology of the anomolous specimen. Rehn and Hebard (1914) listed a specimen of *Insara elegans consuetipes* (Scudder) as a gynandromorph, but I have seen this specimen at the Academy of Natural Sciences of Philadelphia and believe it was merely deformed slightly during its final moult. Some specimens described as bilateral gynandromorphs showed some degree of dorso-ventral gynandromorphism (Ramme, 1913; Potter, 1940; Friauf, 1947; Pener, 1964). A gynandromorph of *Camnula pellucida* (Scudder) exhibited the left ventral valve and right dorsal and ventral valves of an ovipositor on an otherwise male abdomen (Paul, 1941). The remaining gynandromorphs were either intersexes or typical bilateral gynandromorphs.

Several authors have detected the anomaly before the specimen was killed (see Table 1) and consequently were able to examine and describe both the external and internal morphology. Forty-three gynandromorphs have been studied internally to date. In only three bilateral specimens is the bilaterality reflected completely both internally and externally (Agar, 1940; Joly, 1959; Harz, 1960). There is only one case of a bilateral gynandromorph in which internal female genitalia are completely lacking (Robertson, 1936), although two other gynandromorphs are predominantly male internally, with only a spermatheca (Potter, 1940) or a reduced ovary (Kimura, 1951) internally. Six gynandromorphs lack internal male genitalia (Carothers, 1939; Pener, 1964; Slifer and King, 1967; Suzuki, 1934). The remaining specimens have both male and female structures internally with conspicuous ovotestes on at least one side. Suzuki (1934) obtained 14 gynandromorphs or intersexes through X-ray irradiation of crosses of *Homoeogryllus japonicus* (de Haan) and on the basis of internal genitalic morphology found six types: 1/2 normal ♂ (♀ absent), normal ♂ (♀ absent), normal ♀ (♂ absent), 1/2 normal ♂, 1/2 ovotestes, 1/2 normal ♀, 1/2 ovotestes, and both sides ovotestes.

Six authors were able to identify gynandromorphs early enough to study their behavior. Carothers (1939) described a bilateral gynandromorph derived from an interspecific laboratory cross of *Trimerotropis citrina* (Scudder) ♂ × *T. maritima* (Harris) ♀. The specimen attracted males and also attempted to court females. Pener (1964) described the sexual behavior of two bilateral gynandromorphs of *Schistocerca gregaria* (Forskål). One specimen attempted unsuccessfully to copulate with females on five separate occasions. This specimen showed no characteristic female behavior, although internally it possessed ovaries with mature ova. The second gynandromorph behaved similarly, attempting copulation four different times. Neither specimen had testes, though both exhibited male behavior. This behavior, however, terminated well before their deaths, and mature ova were present at the time of deaths, suggesting a possible switch in behavior based on the internal maturation of female sex organs. Slifer (1966) reported on egg-laying by a gynandromorph of *Melanoplus differentialis* (Thomas). Since the specimen was a virgin bilateral gynandromorph, the eggs were unfertilized. Nevertheless, one egg hatched from a clutch of 52. Harz (1960) reported for the first time on sound production by a tettigoniid bilateral gynandromorph, *Metrioptera brachyptera* (L.). The stridulations resembled those of normal males. This specimen behaved like a male in the presence of females, courting and attempting copulation with a nearby female. It was not attracted to the stridulations of a male of the same species. Omachi (1929) mentions that intersexes (dorsoventral gynandromorphs with male abdomens and female tegmina) of *Homoeogryllus japonicus* also behaved like males, extruding spermatophores, pursuing females, and raising their tegmina as if to stridulate.

The biological causes of gynandromorphism have been reviewed in some detail by Morgan and Bridges (1919). Four interpretations have been advanced. Boveri (1888) suggested the *partial fertilization* hypothesis, in which a spermatozoan might be delayed in penetrating the egg until after cleavage had commenced. Subsequent fertilization of one of the daughter nuclei would result in diploid cells (which would become the female portion of the organism), while the unfertilized daughter nucleus would result in haploid cells (which would become the male portion). Some Hymenoptera gynandromorphs may have originated from partial fertilization (Whiting and Whiting, 1927).

A second interpretation, advanced by Morgan (1905), is *dispermy* (or *polyspermy* of some authors). In this case, the egg might be penetrated by more than one spermatozoan, one of which would fertilize the egg nucleus, forming diploid (= female) daughter cells, while the other spermatozoan would develop on its own, forming haploid (= male) daughter cells.

Doncaster (1914) suggested dispermy of a *binucleated egg*. He observed that some eggs have two nuclei and surmised that if each were united by a spermatozoan, one of the male-producing variety (either Y or no-X) and one of the

Table 1. Published records of gynandromorphs in the saltatorial Orthoptera.

SPECIES	REFERENCE	♂ SIDE	♀ SIDE	DEGREE OF GYNANDROMORPH	SOURCE OF SPECIMEN	DESCRIPTION OF INTERNAL ANATOMY
TETRIGIDAE						
Paratettix texanus Hancock [= *P. cucullatus* (Burmeister)] (Tetriginae)	Robertson 1936	left	right	bilateral	laboratory colony	yes
ACRIDIDAE						
Anacridium moestrum (Serville) (Cyrtacanthacridinae)	Potter 1940	left	right	all male dorsally, bilateral ventrally	laboratory colony	yes
Cammula pellucida (Scudder) (Oedipodinae)	Paul 1941	-	-	mainly male, with female accessory structures	field collected	no
Cammula pellucida (Scudder) (Oedipodinae)	Friauf 1947	left	right	all male dorsally, bilateral ventrally	field collected	no
Chorthippus biguttulus (L.) (Gomphocerinae)	Ebner 1951	-	-	parasite-induced intersex	field collected	no
Chorthippus biguttulus (L.) (Gomphocerinae)	Oschmann 1971	right	left	mainly female, with accessary male structures	field collected	no
Chorthippus longicornis (Latreille) (Gomphocerinae)	Karaman 1959	--	--	mainly female, with accessary male structures	field collected	no
Chorthippus longicornis (Latreille) (Gomphocerinae)	Oschmann 1971	left	right	bilateral	field collected	no
Chorthippus montanus (Charp.) (Gomphocerinae)	Bednarz 1970	right	left	bilateral	field collected	yes
Chrysochraon dispar (Germar) (Gomphocerinae)	Brisout de Barneville 1847, 1848a	-	-	mainly male, with female structures	field collected	no
Euchorthippus pulvinatus gallicus Maran (Gomphocerinae)	Descamp 1968	-	-	parasite-induced intersex	field collected	yes
Locusta migratoria L. (Oedipodinae)	Joly 1959	right	left	bilateral	laboratory colony	yes
Locusta migratoria L. (Oedipodinae)	Verdier 1960	left	right	bilateral	?	no
Locusta migratoria L. (Oedipodinae)	Verdier unpubl. (in Uvarov 1966)	right	left	bilateral	laboratory colony	no
Melanoplus adelogyrus Hubbell (Melanoplinae)	Hubbell 1932	right	left	bilateral	field collected	no
Melanoplus differentialis (Thomas) (Melanoplinae)	Slifer 1966	left	right	bilateral	laboratory colony	yes
Melanoplus differentialis (Thomas) (Melanoplinae)	Slifer and King 1967	left	right	bilateral	laboratory colony	yes
Melanoplus fasciatus (Walker) (Melanoplinae)	White and Rock 1945	right	left	bilateral	field collected	no
Melanoplus mexicanus mexicanus (Saussure) (Melanoplinae)	Severin 1943	left	right	bilateral	field collected	no
Melanoplus mexicanus mexicanus (Saussure) (Melanoplinae)	Severin 1955	left	right	bilateral	field collected	no
Oedaleonotus phryneicus Hebard (Melanoplinae)	Hebard 1919	left	right	bilateral	field collected	no
Oedaleus inornatus Schulthess (Oedipodinae)	Ritchie 1978	-	-	mainly male externally and internally; some female characters in external genitalia	field collected	yes
Oxya velox (F.) (Oxyinae)	Kimura 1951	-	-	all male, with accessory female structure	laboratory colony	yes
Pardalophora phoenicoptera (Burmeister) (Melanoplinae)	Friauf 1947	-	(right)	all male, with accessory female structure	field collected	no
Podisma pedestris L. (Podisminae)	Baccetti 1954	left	right	bilateral	field collected	no
Podisma sapporoense Shiraki (Podisminae)	Natori 1931	-	-	all male, with accessory female structure	laboratory colony	yes

Table 1. Published records of gynandromorphs in the saltatorial Orthoptera (cont.).

SPECIES	REFERENCE	♂ SIDE	♀ SIDE	DEGREE OF GYNANDROMORPH	SOURCE OF SPECIMEN	DESCRIPTION OF INTERNAL ANATOMY
Schistocerca gregaria (Forskål) (Cyrtacanthacridinae)	Dirsh 1957	right	left	bilateral	laboratory colony	yes
Schistocerca gregaria (Forskål) (Cyrtacanthacridinae)	Pener 1964	right	left	all male dorsally, bilateral ventrally	laboratory colony	yes
Schistocerca gregaria (Forskål) (Cyrtacanthacridinae)	Pener 1964	left	right	bilateral	laboratory colony	yes
Schistocerca paranensis (Burmeister) (Cyrtacanthacridinae)	Morales Agacino 1957	right	left	bilateral	field collected	no
Sphingonotus caerulans (L.) (Oedipodinae)	Dirsh 1957	–	–	mainly male, with accessory female structures	laboratory colony	no
Stauroderus [= *Chorthippus*] *rammei* Ebner (Gomphocerinae)	Ebner 1940	–	–	parasite induced intersex; mainly male, with some female features	field collected	no
Trimerotropis citrina (Scudder) x *T. maritima* (Harris) (Oedipodinae)	Carothers 1939	left	right	bilateral	hybrid cross	yes
Valanga irregularis (Walker) (Cyrtacanthacridinae)	White 1968	left	right	bilateral	field collected	yes
TETTIGONIIDAE						
Acridopeza reticulata Guer. (Phaneropterinae)	Agar 1940	right	left	bilateral	field collected	yes
Amblycorypha oblongifolia (De Geer) (Phaneropterinae)	Pearson 1927, 1929	–	–	all male, with internal female structures	field collected	yes
Amblycorypha oblongifolia (De Geer) (Phaneropterinae)	Pearson 1927, 1929	–	–	all male, with internal female structures	field collected	yes
Amblycorypha rotundifolia (Scudder) (Phaneropterinae)	Pearson 1927 1929	left	right	bilateral	field collected	yes
Barbistes constrictus Brunner von Wattenwyl (Phaneropterinae)	Chladek 1968	left	right	bilateral	field collected	no
Barbistes yersini Brunner von Wattenwyl (Phaneropterinae)	Brunner von Wattenwyl 1876	left	right	bilateral	field collected	no
Decticus albifrons (F.) (Decticinae)	Boudou-Saltet 1975	–	–	mainly female, with intersexual characters in abdomen; internally, ovitestis on left, ovary on right	not mentioned, but presumedly field collected	yes
Decticus verrucivorus (L.) (Decticinae)	Ramme 1951	left	right	bilateral	field collected	no
Ephippiger ephippiger (Fiebig) (Ephippigerinae)	Dumortier 1962	(right)	–	mainly female, left ovipositor valves reduced; internally, right normal male, left normal female genitalia	field collected	yes
Ephippiger ephippiger (Fiebig) (Ephippigerinae)	Dumortier 1962	(right)	(left)	mainly female, with male features internally	field collected	yes
Ephippiger terrestris Yersin (Ephippigerinae)	Kheil 1914	right	left	bilateral	field collected	no
Ephippiger vitium Serville [= *E. ephippiger* (Fiebig)] (Ephippigerinae)	Pantel and de Sinety 1908	–	–	not described	field collected	no
Insara elegans consuetipes (Scudder) (Phaneropterinae)	Rehn and Hebard 1914	–	–	discounted, not a gynandromorph	field collected	no
Isophya modesta (Frivaldsky) (Phaneropterinae)	Kiss 1960	right	left	bilateral	field collected	no
Isophya modesta (Frivaldsky) (Phaneropterinae)	Kiss 1960	–	(left)	mainly male, with female structures on left	field collected	no
Isophya modesta (Frivaldsky) (Phaneropterinae)	Kiss 1960	–	–	mainly male, with tegmina similar to female	field collected	no

Table 1. Published records of gynandromorphs in the saltatorial Orthoptera (cont.).

SPECIES	REFERENCE	♂ SIDE	♀ SIDE	DEGREE OF GYNANDROMORPH	SOURCE OF SPECIMEN	DESCRIPTION OF INTERNAL ANATOMY
Isophya pavelii Brunner von Wattenwyl (Phaneropterine)	Brunner von Wattenwyl 1876	left	right	bilateral	field collected	no
Isophya pyrenaea (Serville) (Phaneropterinae)	Dumortier and Paly 1971	right	left	bilateral	field collected	no
Leptophyes punctatissima (Bosc) (Phaneropterinae)	Cappe de Baillon 1924	left	right	bilateral	field collected	yes
Leptophyes punctatissima (Bosc) (Phaneropterinae)	Cappe de Baillon 1932	left	right	bilateral	field collected	yes
Metrioptera brachyptera (L.) (Decticinae)	Cappe de Baillon 1924	left	right	bilateral	field collected	yes
Metrioptera brachyptera (L.) (Decticinae)	Ebner 1940	-	-	male with some characters similar to female	field collected	no
Metrioptera brachyptera (L.) (Decticinae)	Harz 1960	left	right	bilateral	field collected	yes
Microcentrum retinerve (Burmeister) (Phaneropterinae)	Nickle, in this paper	right	left	bilateral	field collected	no
Odontura sp. (Phaneropterinae)	Chadima 1872	left	right	bilateral	field collected	no
Paeciliman elegans Brunner von Wattenwyl (Phaneropterinae)	Ramme 1926	(left)	-	all female, with accessory male structure	field collected	no
Paeciliman orbeliscus Panc (Phaneropterinae)	Harz 1967	right	left	bilateral	field collected	yes
Pycnogaster graëllsi Bolivar (Pycnogastrinae)	Pantel and de Sinety 1908	-	-	not described	field collected	no
Tettigonia viridissima (L.) (Tettigoniinae)	Klapalek 1897	?	?	reference not seen by author	field collected	no
Thmanotrizon [=*Pholidoptera*] *fallax* (Fitsch) (Decticinae)	Ramme 1913	right	left	mainly male dorsally, bilateral ventrally	field collected	yes
GRYLLACRIDIDAE						
Dolichopoda linderi Duf. (Rhaphidophorinae)	Saltet 1968	right	left	bilateral	field collected	yes
GRYLLIDAE						
Gryllus [as *Acheta bimaculatus* De Geer x *campestris* L.) x *bimaculatus* (Gryllinae)	Cousin 1935, 1937	-	-	mainly female, with some intersexual characters on tegmen and genitalia	hybrid cross	yes
Gryllus (*argentinus* Saussure x *capitatus* Saussure) x *capitatus* (Gryllinae)	Cousin 1967	right	left	bilateral	hybrid cross	no
Gryllus bimaculatus De Geer (Gryllinae)	Johnstone 1975	left	right	bilateral, with intersex characters on tegmen	laboratory colony	yes
Gryllus lineaticeps Walker (Gryllinae)	Chopard 1955	-	-	intersex	field collected	yes
Gryllus bimaculatus De Geer x *capitatus* Saussure - back crosses:	Cousin 1963					
1. *BC*♀ x *BB*♂		right	left	bilateral	hybrid cross	yes
2. *BC*♀ x *CC*♂		right	left	bilateral	hybrid cross	yes
Homoeogryllus japonicus (de Haan) (Phalangopsinae)	Ohmachi 1929	-	-	29 specimens: 4 bilaterals (not described), 18 males with female tegmina, 4 males with tegmina having intersexual characters, 3 males with female tegmina and female internal structures	laboratory colony	yes
Homoeogryllus japonicus (de Haan) (Phalangopsinae)	Ohmachi 1932	-	-	405 offspring described as intersexes, in most cases mainly males with female or intersex tegmina	hybrid crosses	yes

Table 1. Published records of gynandromorphs in the saltatorial Orthoptera (cont.).

SPECIES	REFERENCE	♂ SIDE	♀ SIDE	DEGREE OF GYNANDROMORPH	SOURCE OF SPECIMEN	DESCRIPTION OF INTERNAL ANATOMY
Homoeogryllus japonicus (de Haan) (Phalangopsinae)	Suzuki 1933	left	right	bilateral	laboratory colony; x-ray irradiated	no
Homoeogryllus japonicus (de Haan) (Phalangopsinae)	Suzuki 1933	–	(right)	mainly male, with female accessory structures	laboratory colony; x-ray irradiated	yes
Homoeogryllus japonicus (de Haan) (Phalangopsinae)	Suzuki 1934	–	–	14 specimens with 6 types of combinations of male and female gonads	laboratory colony; x-ray irradiated	yes
Madassuma [=*Xenogryllus*] *marmoratus* Haan (nec Bolivar) (Eneopterinae)	Ohmachi 1926	right	left	bilateral, with some intersexual characters	laboratory colony	yes

female-producing variety (X), then all daughter cells would be diploid but give rise to male and female sides.

Morgan (1914) proposed *chromosomal elimination*, for which an abundance of evidence has since accumulated. According to this interpretation, the gynandromorph begins development as a normal female zygote, but during an early cleavage one of the X-chromosomes is eliminated or fails to migrate to the daughter nucleus. This results in all subsequent cells being male (i.e., X-0) while the cells from the normal initial cell will be female (X-X).

Among the cases of gynandromorphism in Orthoptera, ten authors have speculated on the biological origin of their specimens. Carothers (1939) considered the gynandromorph offspring of a cross between *Trimerotropis maritima* and *T. citrina* to be the result of either the chromosomal elimination of an X-chromosome and one or more autosomes or dispermy in which diploidy was restored as in parthenogenesis and one X-chromosome was eliminated or else never doubled when the autosomes did. She felt the first alternative was unlikely to cleave successfully and suggested that the second was more probable. Slifer (1966) suggested that her gynandromorph of *Melanoplus differentialis* began as a female, but early in mitotic cleavages of the zygote an X chromosome was lost from a cell from which most of the left side developed. Since this error in cleavage failed to account for the absence of testes on the left, she considered a second error occurred later, resulting in elimination of cells from which male internal organs are derived. Ohmachi (1926) similarly explained his gynandromorph of *Madasumma marmorata* de Haan.

Johnstone (1975) also combined the elimination of an X chromosome with a second event, in her case, the mingling of male and female cells during gastrulation to form mosaic regions. Pearson (1929) reviewed the four hypotheses to account for gynandromorphism and concluded that either dispermy of binucleated eggs or chromosomal elimination could account for his specimens of *Amblycorypha* species. He suggested that additional gains or losses of autosomes could also influence the expression of sex (see Carothers' specimen as an example). Cappe de Baillon (1924) and Cousin (1963) also suggested that elimination of the X chromosome at an early mitotic division was the cause of their respective gynandromorphs. White (1968), on the other hand, presented evidence for dispermy of a binucleated egg. Since his specimen differed bilaterally not only for sex expression but also for non-sex-linked color pattern, he considered dispermy of a binucleated egg the only possible alternative. Finally, Ebner (1940, 1951) demonstrated that in some cases of specimens displaying secondary sexual characters of the opposite sex, the cause may be attributed to actions of parasites of the specimen at some stage in its development. He described several specimens of grasshoppers that were predominantly male but had tegmina and cerci that were more typically female in structure.

A Gynandromorph of the Lesser Angle-winged Katydid

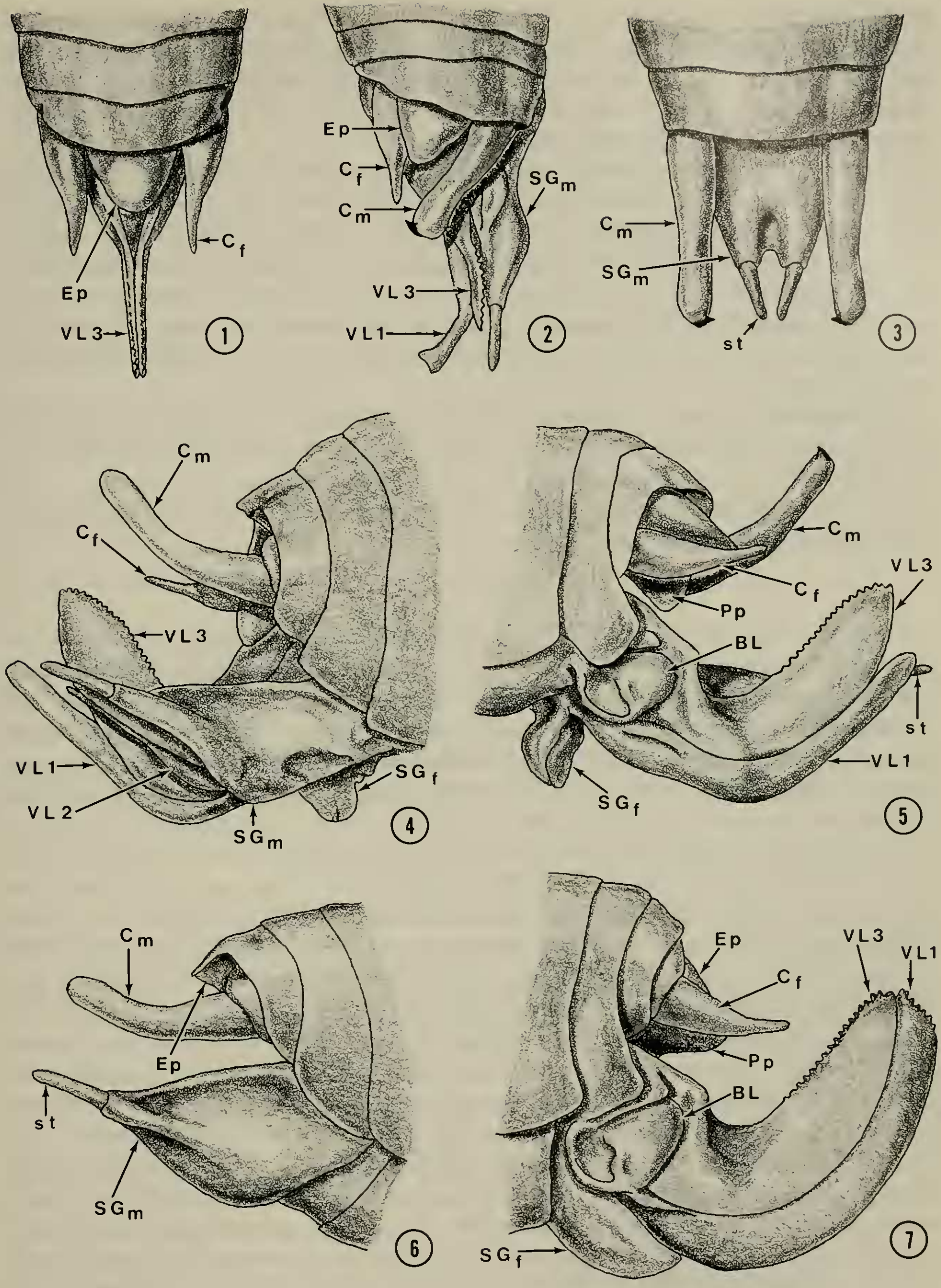
On 4 September 1970 a bilateral gynandromorph of the lesser angle-winged katydid, *Microcentrum retinerve* (Burmeister) [Tettigoniidae; Phaneropterinae], was collected by the author at Lake Drummond, Dismal Swamp, Nansemond Co., Virginia. The specimen was collected along with seven normal males and four normal females at an incandescent light source. It was unfortunately not recognized as a bilateral gynandromorph until after the specimens had been prepared for dry mounting on pins.

The specimen is a well-defined bilateral gynandromorph with male characters on the right side of the body, female on the left. Minor differences in proportion reflecting the expression of each sex occur in the face, pronotum, and abdominal tergites. The distortion of the face is reflected in the typically larger compound eye on the male side which in contrast also has shorter lower facial features than the female side, resulting in torsion of the clypeus and labrum toward the male side.

The tegmina display sexual differences on each side of the body. The right tegmen is typically male, possessing a pars stridens or scraper along the anal margin and a ventrally-located non-functional stridulatory file. Normal males also possess this structure, and no measurable differences are noted between the gynandromorph and normal males for any structures on the right tegmen. The left tegmen is typically female, with a thickened sharp scraper on the anal margin (Nickle and Carlysle, 1975). The tegmina of this katydid show none of the intersexual characteristics described by Johnstone (1975); instead, each tegmen falls within the normal range of variation for its respective sex.

The most apparent gynandromorphic features are expressed in the external genitalia. In a normal male (Figs. 3, 6) the tenth tergite is slightly produced and apically truncate, with the epiproct recessed and articulating ventrally from the tenth tergite. The cercus is long, cylindrical, and tapering distally, with a preapical medially-directed dark tooth. The subgenital plate is broad, with an apical, median U-shaped emargination and two lateral well-developed styles. The normal female abdomen (Figs. 1, 7) also has a truncate terminal tergite with a more posteriorly-directed epiproct. The cercus is simple, distally tapered and lacking a tooth. The ovipositor is moderately developed, nearly as long as the pronotal disc (5–6 mm), acutely upcurved and serrate along the distal half of the dorsal valve and at the apex of the ventral valve. The subgenital plate is basally broad, becoming increasingly constricted distally and apically nearly pointed.

The external genitalia of the gynandromorph (Figs. 2, 4, 5) have all the typical male parts on the right side and female parts on the left, although there are considerable distortion and some size differences compared with normal male and female genitalia. The male tenth tergite is complete but reduced in length on



Figs. 1–7. Abdomens of *Miocrocentrum retinerve.* 1, 7, Normal female. 3, 6, Normal male. 2, 4, 5, Gynandromorph. 1–3 dorsal views; 4, 6 right lateral views; 5, 7 left lateral views. Ep = epiproct; Pp = paraproct; C_m and C_f = cercus of male and female, respectively; VL1, VL2, VL3 = valvula 1, 2, and 3 of ovipositor, respectively; SG_m, SG_f = male and female subgenital plate, respectively; st = style of male subgenital plate; BL = basal lobe of ovipositor.

the female side. Although the male cercus is not distorted, it is only ⅔ as long as a normal male cercus. Only the right half of the male subgenital plate is present, and in structure its base is nearly identical with the base of the female ventral valve of the ovipositor on the left side; distally, it shows all the characteristics typical of a normal male subgenital plate.

The ovipositor of the female side is much distorted, in part from gynandromorphic asymmetry and in part from drying. The distal half of the dorsal valve shows little distortion, but the distal half of the ventral valve bears little resemblance to the normal form, is apically truncate, and completely lacks apical serrations. The basal lobe of the ovipositor is nearly the same in shape but smaller than the normal form. The subgenital plate of the female side is reduced to a cup-shaped plate on the left side and becomes confluent with the subgenital plate on the male side.

Measurements (mm).—Values for ♂ and ♀ are means of 10 individuals for each sex. Length of forefemur ♂ 4.90; ♀ 5.34; ⚥R 4.95; ⚥L 5.27. Length of midfemur, ♂ 7.30; ♀ 7.68; ⚥R 7.53; ⚥L 7.84.

The specimen has been donated to the National Museum of Natural History, Washington, D.C.

Discussion

The occurrence of gynandromorphism in Orthoptera is most likely an aberration with no adaptive significance. Certainly bilateral gynandromorphs are unlikely to reproduce successfully, since copulation is physically not possible, at least for specimens so far examined. Nevertheless, it is possible that a genetic propensity for gynandromorphism could be maintained within a gene pool, if there were selection for heterosis with strong positive pleiotropic effects, and the gynandromorphs were at least as reproductively successful as normal individuals.

Most reports of gynandromorphism are among laboratory crosses (Ohmachi, 1929, 1932; Suzuki, 1934; Pener, 1964; Slifer, 1966; Slifer and King, 1967) or among interspecific hybridization studies (Carothers, 1939; Cousin, 1967), and inbreeding and artificial selection for such a character complex is likely to be common only under such artificial conditions. Nevertheless, in two cases, gynandromorphs or intersexes appear at higher frequencies than one would expect. Ohmachi (1929) listed 25 *Homoeogryllus japonicus* intersexes which were incapable of sound production but apparently capable of producing spermatophores. These specimens apparently were secured from a professional insect breeder. Ohmachi (1932) also demonstrated that when these intersexes were crossed with normal individuals, both normal and intersex offspring were produced. Such specimens in nature would seem to be less likely to be successful than normal calling males in obtaining mates. However, if the density of the population were so high that visual contact were as likely as attraction to conspecific calling signals in getting males and females together, or if such non-singing individuals could compete favorably as interlopers for females responding to singing males, or if selection favored "non-singing" or pantomiming males, as perhaps an adaptation to avoid predation or parasitization from natural enemies with an auditory search image, intersexes of this species may be reproductively successful competitors with normal individuals. This has not been demonstrated in nature, however.

Pearson (1927, 1929) described three field-collected gynandromorphs detected from a rather small sampling of *Amblycorypha rotundifolia* (Scudder) and *A. oblongifolia* (De Geer). Two of these proved to be intersexes that were externally males capable, at least morphologically, of self fertilization and of cross-fertilization with normal females. If self fertilization were possible, its adaptive significance would be similar to animals with facultative parthenogenesis (Nabours, 1919; Roth and Willis, 1956, 1961). Such an adaptation would permit females to produce viable offspring in periods when mates may not be available or when it would be otherwise advantageous for the female to invest completely in her offspring by providing 100% of the genetic material. In species of *Amblycorypha*, populations are frequently low, and species are exploitive, occupying new habitats such as weedy new growth. Finding mates in such situations may be unlikely at times, and dangerous if the time invested in waiting for mates reaches a level such that predation becomes more likely, so that a predisposition toward intersexuality or facultative parthenogenesis may be adaptive. Since Pearson's internal gynandromorphs were externally males, they would not be expected to successfully oviposit eggs, even if they were successful in self fertilization. If the reciprocal gynandromorph were possible, i.e., a female capable of self fertilization internally, successful reproduction could result from such an anomaly. Certainly more research on this group is needed to demonstrate such an adaptation.

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Literature Cited

Agar, W. E. 1940. A gynandromorph grasshopper. Proc. Zool. Soc. Lond. 109A: 139–40.

Baccetti, B. 1954. Su un caso di ginandromorfismo in *Podisma pedestris* L. (Orth. Catant.). Redia 39: 401–411.

Balazuc, J. 1948. La teratologie des coleoptères et experiences de transplantation sur *Tenebrio molitor* L. Mem. Mus. Natl. Hist. Nat. (n.s.) 25: 1–293.

———. 1952. Un *Ergates faber* L. gynandromorphe [Col., Cerambycidae]. Bull. Soc. Entomol. Fr. 57: 34–38.

Balazuc, J. and H. Donnot. 1953. Nouvelle anomalie sexuelle chez un Longicorne [Col., Cerambycidae]. Bull. Soc. Entomol. Fr. 58: 95-96.

Bednarz, S. 1970. A case of gynandromorphism in *Chorthippus* (*Chorthippus*) *montanus* (Charp.) (Orthoptera Acridioidea). Zool. Pol. 20: 81–86.

Bertkau, P. 1889. Beschreibung eines Zwitter von *Gastropache quercus* nebst allgemeinen Bemerkungen und einem Verzeichniss der beschreibenen Arthropoden Zwitter. Ark. Naturgesch. 55: 75–116.

Blanchard, A. 1969. A gynandromorphic *Phaeoura mexicanaria* (Geometridae). J. Lepid. Soc. 23: 274–275.

Boveri, T. 1888. Uber partielle Befruchtung. Sitzungsber. Ges. Morphol. Physiol., Munch., Bd. 4: 64–72.

Brisout de Barnville. 1847. Description de l'*Acridium smilaceum*, individu hermaphrodite. Ann. Soc. Entomol. Fr. 5: 86.

———. 1848a. Description de l'*Acridium smilaceum*, individu hermaphrodite. Ann. Soc. Entomol. Fr. 6: 38.

———. 1848b. *Acridium* (=*Chrysochraon*) *dispar* hermaphrodite. Ann. Soc. Entomol. Fr. 6: 54.

Brunner von Wattenwyl, C. 1876. Die morphologische Bedeutung der Segmente, speciell des Hinterleibes, bei den Orthopteren. 18 pp.

Boudou-Saltet, P. 1968. Sur un *Dolichopoda* (Orth. Rhaph.) gynandromorphe. Bull. Soc. Hist. Nat. Toulouse 104: 165–178.

———. 1975. Un *Decticus albifrons* (Orth. Tett.) gynandromorphe. Bull. Soc. Hist. Nat. Toulouse 111: 160–164.

Cappe de Baillon, P. 1924. Recherches sur le gynandromorphism. *Metrioptera brachyptera* L. et *Leptophyes punctatissima* Bosc. Cellule 34: 69–132.

———. 1932. Gynandromorphes de *Leptophyes punctatissima* Bosc. [Orth. Phasgonuridae]. Bull. Soc. Entomol. Fr. 38: 177–181.

Carothers, E. E. 1939. A hybrid acridian gynandromorph. Genetics 24: 97.

Chadima, J. 1872. Ueber die Homologie zwischen den männlichen und weiblichen äussern Sexualorganen der Orthoptera Saltatoria Latr. Mitteil des Naturwiss. Verh. Sturmark. 25–33.

Chladek, F. 1968. Gynandromorf kobylky *Barbistes constrictus* Br. W. 1878. Zpravy Cs. Spolecnosti Entomol. pri Csav, Praha 3–4: 57–58.

Chopard, L. 1938. La Biologie des Orthopteres. Paris. 541 pp. (Pp. 222–238).

———. 1955. Note sur un Grillon gynandromorphe provenant du Congo Belge. Mem. Soc. R. Belg. Entomol. 27: 153–157.

Cousin, G. 1935. Sur un cas de gynandromorphisme chez un hybride de Gryllides (♀ *Achaeta bimaculata-campestris* × ♂ *A. bimaculata*). C. R. Acad. Sci. 200: 348.

———. 1937. Sur quelques anomalies de developpement chez les Gryllides. C. R. Congr. Soc. Sav-Paris 70: 215–222.

———. 1963. Hybridation et gynandromorphisme chez les Gryllides. Bull. Soc. Entomol. Fr. 68: 106–12.

———. 1967. Quelques points de vue sur l'hybridation chez les animaux. Bull. Soc. Zool. Fr. 92: 441–484.

Descamps, M. 1968. Notes sur le genre *Euchorthippus* [Orth. Acrididae], sa repartition dans le Vaucluse et les departements adjacents. Ann. Soc. Entomol. Fr. (n.s.) 4: 5–25.

Dirsh, V. M. 1957. Two cases of gynandromorphism in Acrididae (Orthoptera). Entomol. Mon. Mag. 93: 193–194.

Doncaster, L. 1914. On the relations between chromosomes, sex-limited transmission, and sex determination in *Abraxas grossulariata*. J. Genet. 4:

Dumortier, B. 1962. Un cas de gynandromorphisme chez *Ephippiger ephippiger* (Fiebig) (Orthopt., Ephippigeridae). Bull. Soc. Zool. Fr. 87: 241–252.

Dumortier, B. and J. Paly. 1971. Sur un individu gynandromorphe d'*Isophya pyrenaea* (Serville). Bull. Soc. Entomol. Fr. 76: 51–54.

Ebner, R. 1940. Veranderungen an Orthopteren durch parasitische Würmer. VIth Int. Congr. Entomol. Proc. 1: 341–347.

———. 1951. Ein neuer Fall von Veraenderunger an einer Heuschrecke (Orthoptera, Acrididae) durch einen Parasiten. Eos 29: 119–22.

Friauf, J. J. 1947. Notes on two orthopteran gynandromorphs. Occas. Pap. Mus. Zool. Univ. Mich. No. 501, 8 pp.

Hagen, H. 1861. Insekten Zwitter. Stettin. Entomol. Zeit. 22: 259–286.

Harz, K. 1960. Orthoptelogische Beitrage III. Nachrichtenbl. Bayer. Entomol. 9: 81–85.

———. 1967. Neues von europaischen Orthopteren. Zool. Beitr. 13: 471–477.

Hebard, M. 1919. New genera and species of Melanopli found within the United States (Orthoptera, Acrididae). Trans. Am. Entomol. Soc. 45: 257–298.

Hessel, S. A. 1964. A bilateral gynandromorph of *Automeris io* (Saturniidae) taken at mercury vapor light in Connecticut. J. Lepid. Soc. 18: 27–31.

Hubbell, T. H. 1932. A revision of the *puer* group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacridinae (Orthoptera, Acrididae). Misc. Publ. Mus. Zool. Univ. Mich. 23, 64 pp.

Johnstone, D. E. 1975. A gynandromorph cricket, *Gryllus bimaculatus* (Grylloptera: Gryllidae). Can. J. Zool. 53: 1505–1513.

Joly, P. 1959. Un cas de gynandromorphisme chez *Locusta migratoria* L. Bull. Soc. Zool. Fr. 84: 407–410.

Karaman, M. 1959. Sur un *Chorthippus longicornis* Latr. (Orthop. Acrididae) hermaphrodite. Bull. Soc. Entomol. Mulhouse 1959: 51–53.

Kheil, N. M. 1914. Orthopterologisches von den Hyereschen Inseln (Hermaphroditismus bei Orthopteren). Int. Entomol. Z. Guben 8: 123–167.

Kimura, Y. 1951. Spontaneous occurrence of testis ova in a grasshopper, *Oxya velox*. Zool. Mag. (Tokyo) 60: 213–215. (Japanese, summary in English.)

Kiss, B. 1960. Gynandromorph *Isophya modesta* Friv. peldayok. (Orthopt., Tettigon.) Rovart. Folia Entomol. Hung. (n.s.) 13: 163–166.

Klapalek, Fr. 1897. Obojetnik kobylky Zelene (*Locusta viridissima* L.). Abh. kon. Bohm. Ges. Wiss. 12: 1–5.

Morales Agacino, E. 1957. The abdominal morphology of a gynandromorph of *Schistocerca paranensis* (Burm.). Proc. R. Entomol. Soc. Lond. (A) 32: 169–170.

Morgan, T. H. 1905. An alternative interpretation of gynandromorphous insects. Science (Wash., D.C.) 21: 632–634.

———. 1914. Mosaics and gynandromorphs in *Drosophila*. Proc. Soc. Exp. Biol. Med. 11:

Morgan, T. H. and C. R. Bridges. 1919. I. The origin of gynandromorphs. Contributions to the Genetics of *Drosophila melanogaster*. Carnegie Inst. Wash. Publ. 278, 222 pp.

Nabours, R. 1919. Parthenogenesis and crossing-over in the grouse locust *Apotettix*. Am. Nat. 53: 131–142.

Natori, B. 1931. On an ovo-testis found in a larva of locust *Podisma sapporense* Sharaki. Trans. Sapporo Nat. Hist. Soc. 12: 1–5.

Nickle, D. A. and T. C. Carlysle. 1975. Morphology and function of female sound-producing structures in ensiferan Orthoptera with special emphasis on the Phaneropterinae. Int. J. Insect Morphol. Embryol. 4: 159–168.

Ohmachi, F. 1926. 175. Preliminary note on a gynandromorph *Madasumma marmorata*. Proc. Imp. Acad. (Tokyo) 2: 554–558.

———. 1929. Preliminary note on a special type of sex-abnormality in *Homoeogryllus japonicus* de Haan (Oecanthidae). Proc. Imp. Acad. (Tokyo) 5: 370–373.

———. 1932. Preliminary note on breeding experiments with male intersexes in *Homoegryllus japonicus* de Haan. Proc. Imp. Acad. (Tokyo) 8: 205–208.

Oschmann, M. 1971. Neue exemplare von geradfluglern mit gynandromorphen Merkmalen. Dtsch. Entomol. Z. 18: 401–404.

Pantel, J. and R. de Sinety. 1908. Sur l'apparition de males et d'heramaphrodites dans les pontes parthenogenetiques des Phasmes. C. R. Acad. Sci. 147: 72.

Paul, L. C. 1941. Intersexuality in *Camnula pellucida* Scudder (Orthoptera). Can. Entomol. 73: 195–196.

Pearson, N. E. 1927. A study of gynandromorphic katydids. Am. Nat. 61: 283–285.

Pearson, N. E. 1929. The structure and chromosomes of three gynandromorphic katydids (*Amblycorypha*). J. Morphol. 47: 531–553.

Pener, M. P. 1964. Two gynandromorphs of *Schistocerca gregaria* Forskal (Orthoptera: Acridoidea): morphology and behaviour. Proc. R. Entomol. Soc. Lond. (A) 39: 89–100.

Potter, E. 1940. A gynandromorph specimen of *Anacridium moestum* (Serv.) Orthoptera, Acrididae. Proc. R. Entomol. Soc. Lond. (A) 15: 41–46.

Ramme, W. 1913. Uber einen Zwitter von *Thamnotrizon fallax* Fisch. (Orth. Tettig.). Sitzungsber. Ges. Naturforsch. Fr. Berl. 2: 83–89.

———. 1926. Ein *Poecilimon*-Weibchen mit accessorischem männlichem cercus (Orth. Tettigon.). Dtsch. Entomol. Z.: 246.

———. 1951. Zur Systematik, Faunistik, und Biologie der Orthopteren von Sudost-Europa and Vorderaisen. Mitt. Zool. Mus. Berl. 27: 1–431.

Rehn, J. A. G. and M. Hebard. 1914. A revision of the Orthopterous group Insarae (Tettigoniidae, Phaneropterinae). Trans. Am. Entomol. Soc. 40: 37–184.

Ritchie, J. M. 1978. A gynandromorph specimen of *Oedaleus inornatus* Schulthess (Orthoptera: Acrididae). Acrida 7: 149–155.

Robertson, W. R. B. 1936. Morphology and cytology of a gynandromorph of *Paratettix texanus*. Am. Nat. 70: 61.

Roth, L. M. and E. R. Willis. 1956. Parthenogenesis in cockroaches. Ann. Entomol. Soc. Am. 49: 195–204.

———. 1961. A study of bisexual and parthenogenetic strains of *Pycnoscelus surinamensis* (Blattaria: Epilamprinae). Ann. Entomol. Soc. Am. 54: 12–25.

Saltet, P. 1968. See Boudou-Saltet, P., 1968.

Schmid, F. 1973. Deux cas de gynandromorphisme chez les Ornithopteres (Lepidoptera, Papilionidae). Can. Entomol. 105: 1549–1551.

Severin, H. C. 1943. A study of a gynandromorph of *Melanoplus mexicanus mexicanus* (Sauss.) (Orthoptera). J. N.Y. Entomol. Soc. 51: 179–183.

———. 1955. A gynandromorph of *Melanoplus mexicanus mexicanus* (Saussure) extreme migratory phase (Orthoptera: Acrididae). Psyche (Camb., Mass.) 62: 104–107.

Slifer, E. H. 1966. A gynandromorph grasshopper that laid eggs (Orthoptera, Acrididae). Entomol. News 77: 149–155.

Slifer, E. H. and R. L. King. 1967. A gynandromorph grasshopper with an ovotestis (Orthoptera, Acrididae). Entomol. News 78: 1–5.

Suzuki, K. 1933. Two cases of sexual abnormalities in *Homoeogryllus japonicus* de Haan. Proc. Imp. Acad. (Tokyo) 9: 548–550.

———. 1934. Gynandromorphs in *Homoeogryllus japonicus* de Haan. Proc. Imp. Acad. (Tokyo) 10: 509–512.

Tweedie, M. 1965. Gynandromorphs—both male and female but not hermaphrodites. Animals (Lond.) 8(1): 22–24.

Uvarov, B. 1966. Grasshoppers and Locusts, Vol. 1. Cambridge. 481 pp. (p. 149).

Verdier, M. 1960. Remarques de teratologie sur la descendance parthenogenetique de *Locusta migr.* Bull. Soc. Zool. Fr. 85: 203–204.

White, M. J. D. 1968. A gynandromorphic grasshopper produced by double fertilization. Aust. J. Zool. 16: 101–109.

White, R. M. and P. J. G. Rock. 1945. A contribution to the knowledge of the Acrididae of Alberta. Sci. Agric. 25: 577–596.

Whiting, P. W. and A. R. Whiting. 1927. Gynandromorphs and other irregular types in *Habrobracon.* Biol. Bull., Marine Biol. Lab., Woods Hole, Mass. 52: 89–117.